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Contact between formerly allopatric subspecies of Grant's gazelle (*Gazella granti* Brooke, 1872) owing to vegetation changes in Tsavo National Park, Kenya

By W. LEUTHOLD

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Abstract

Studied was range expansion of *Gazella granti petersi* Günther, 1884, in Tsavo East National Park, Kenya, induced by extensive transformation of original *Acacia-Commiphora* woodlands into grass-dominated vegetation types. This, and probably a concurrent range expansion of *G. g. serengetae* Heller, 1913, in Tsavo West National Park resulted in occasional contacts between individuals of the two morphologically distinct subspecies of Grant's gazelle, which were formerly separated by a broad belt of unsuitable habitat.

Introduction

Because of considerable variations in coat colour and horn shape Grant's gazelle (*Gazella granti* Brooke, 1872) has been subdivided into at least nine subspecies (GENTRY 1971). However, few of these are clearly recognizable in the field, and their ranges are but poorly known

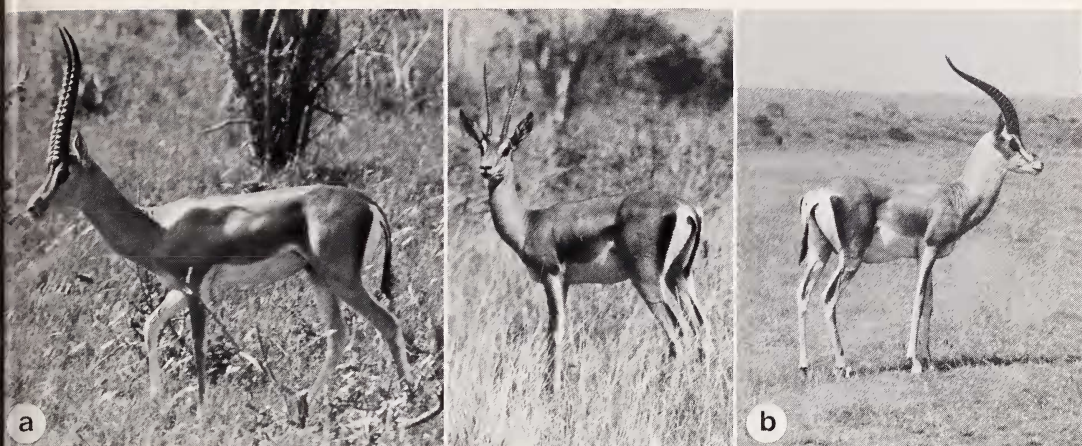


Fig. 1. a: *Gazella granti petersi*. Left: ♂, right: ♀. Note nearly straight horns of ♂ (not fully adult) and dark band dividing the white rump patch. b: *G. g. granti*, adult ♂, Nairobi National Park. Note stronger curve of horns, undivided rump patch and white upperside of tail

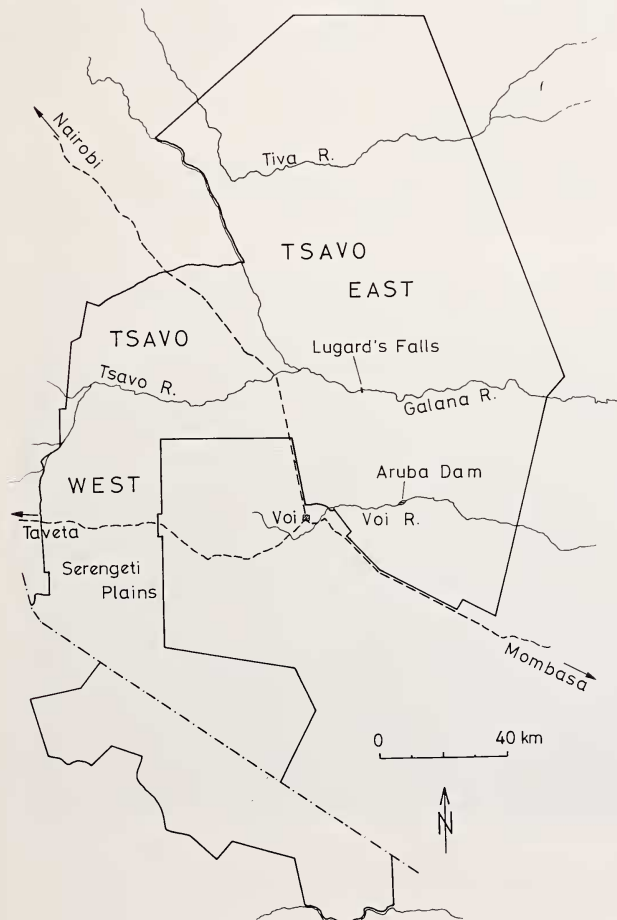


Fig. 2. Map of Tsavo National Park, showing names of localities mentioned in the text

- = park boundary
- - - = Kenya/Tanzania border
- - - = roads and railway lines

(DORST and DANDELLOT 1970; HALTENORTH and DILLER 1977). Also, individuals differ considerably within local populations (WALTHER 1972), which raises doubts about the validity of at least some of the subspecies (= ssp.) described. Possibly the most distinct ssp. is Peters' gazelle (*G. g. petersi* Günther, 1884), with relatively short and straight horns of very narrow spread and a well-defined fawn-coloured band extending from the back to the tail (Fig. 1 a); in most other ssp. the white rump patch continues uninterrupted above the tail (Fig. 1 b). Peters' gazelle inhabits arid areas in eastern Kenya and parts of the adjacent countries and occurs in the eastern section of Tsavo National Park (Fig. 2).

In Tsavo West National Park there is a clearly different ssp. which, according to GENTRY (1971), would be *G. g. serengetae* Heller, 1913. It resembles the nominate ssp. (*G. g. granti* Brooke, 1872), with a slight purplish hue, thicker and more strongly curved horns, somewhat larger size and heavier build than *petersi* (Fig. 1 b). Its subspecific name does not, as is sometimes assumed, refer to the well-known Serengeti area in Tanzania, but to the Serengeti Plains near Taveta in south-eastern Kenya, which is the type locality (Fig. 2). LYDEKKER and BLAINE (1914), however, also list two specimens of *G. g. granti* as originating from Taveta (skulls only). My use of the name *serengetae* does not imply recognition of its taxonomic validity.

Very probably, *G. g. petersi* and *G. g. serengetae* were entirely allopatric until recently, although the line or area of separation is not clearly known. The formerly dense *Acacia-Commiphora* woodlands of the Tsavo area probably constituted an effective barrier. Their large-scale transformation into fairly open, grass-dominated vegetation types (Fig. 3), under the influence of elephants and fire (e. g. NAPIER BAX and SHELDRIK 1963; LEUTHOLD 1979), enabled the gazelles to move into areas previously not inhabited by them. When Tsavo National Park was established in 1948, "Peters' gazelle . . . [was] . . . confined to the northern area and never seen south of the Galana River" (SHELDRIK 1973, p. 112). By the time I began field work in Tsavo East in late 1968, it had become well established north-east of a line from Aruba to Lugard's Falls (Fig. 2), as well as to the south of the Voi River, where the most open habitats existed (see Map 1 in NAPIER BAX and SHELDRIK 1963; LEUTHOLD and LEU-



Fig. 3. Aerial view of park boundary north of Voi (August 1971). Left: *Acacia-Commiphora* woodland which, inside the park (right), has been replaced by fairly open bushy grassland. Centre: Railway line to Nairobi.

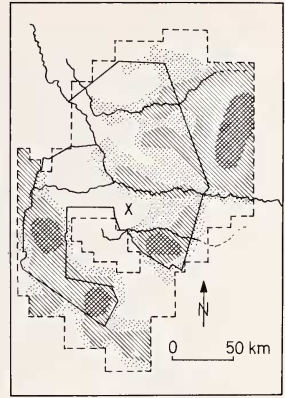


Fig. 4. Density distribution of Grant's gazelle in the Tsavo area in 1973/74 (after COBB 1976). Cross-hatching = high density; simple hatching = medium density, stippling = low density. Broken line = boundary of census area, X = present study area (cf. Fig. 5). Note "corridor" between *G. g. serengetae* (lower left) and *G. g. petersi* (upper right)

THOLD 1976). Gross distribution patterns derived from a series of aerial counts made in 1973/74 (COOB 1976) approximately reflect this situation (Fig. 4), showing, firstly, a clear gap between the ranges of *petersi* and *serengetae* and, secondly, the absence of gazelles in the westernmost part of Tsavo East (area marked X in Fig. 4). Detailed monitoring of the range expansion was possible only through long-term observations on the ground. Between 1969 and 1974 I noted sightings of Peters' gazelle with a view to documenting its presumed advance into the area concerned.

Methods

In late 1968 Peters' gazelle was regularly seen near Aruba (Fig. 2) and 10–15 km westward along the Voi River, and along the Galana River as far west as Lugard's Falls. I therefore concentrated on the area depicted in Figure 5.

Two sets of observations were collected:

- Records of Peters' gazelle seen in the course of 15 systematic game counts along park roads, five in each year from 1969 to 1971 ("road counts", LEUTHOLD and LEUTHOLD 1975, 1976);
 - Unsystematic records of sightings made while working on other studies in the area concerned.
- The data from the road counts are directly comparable from year to year, as the same roads were covered within 2–3 days on each occasion. Data in set (b) are more difficult to interpret, as no systematic pattern was followed, some areas being visited much more frequently than others. This, however, increased the chances of actually seeing gazelles that had moved into a "new" area.

Results

Immigration of *G. g. petersi*

Figure 5 shows all sightings of Peters' gazelle in the study area from 1969 to 1973, separated as to year and type of observation; Table 1 gives the number of sightings recorded in each year.

Firstly, there appears to be a gradual increase in the number of sightings per year over the first four years.

Secondly, the earliest observations were made either near the Galana River or at Irima (Fig. 2) near the Voi River, whereas locations more central to the study area were apparently reached by gazelles only in 1972/73. A possible exception is the area along the Voi River (see Discussion).

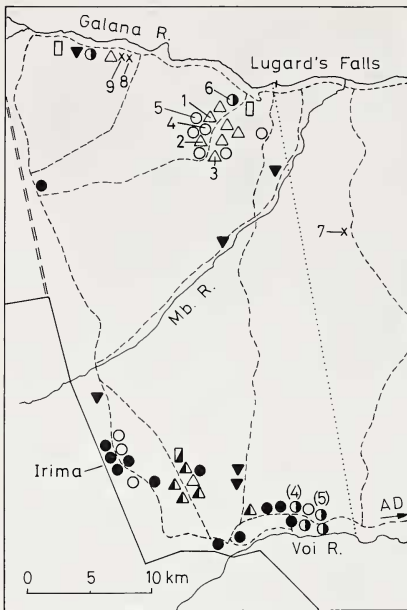


Fig. 5. Map of study area with sightings of Grant's gazelles. Only observations west of the dotted line are indicated (exception: No. 7). Numbered locations refer to *G. g. serengetae* (cf. Table 2). Figures in parentheses indicate multiple sightings in same location. X = records of *G. g. serengetae* outside area (No. 7) or period (Nos. 8 + 9) referred to otherwise. Mb. R. = Mbololo River

- = 1969, road counts
- ◼ = 1969, casual observations
- △ = 1970, road counts
- ▲ = 1970, casual obs.
- = 1971, road counts
- = 1971, casual obs.
- = 1972, casual obs. only
- ▼ = 1973, casual obs. only

Table 1

Sightings of Peters' gazelle in the westernmost part of Tsavo East National Park

The area depicted in Fig. 5

	1969	1970	1971	1972	1973
road counts	2	9	10	—	—
Unsystematic records	1	5	13	12	6

Sightings of *G. g. serengetae* in Tsavo East

As far as I know, *G. g. serengetae* had never been recorded inside Tsavo East (cf. Fig. 4) when, on 29 April 1970, my wife and I observed a nearly adult ♂ *serengetae*, together with a ♂ and 2 ♀♀ *petersi*, ca. 6 km SW of Lugard's Falls (No. 1 in Fig. 5). Of particular interest was the fact that the two ♂♂ — of clearly distinct ssp. — engaged in several bouts of light fighting, and the *serengetae* ♂ showed sexual displays (head and tail raised, stiff-legged walk; WALTER 1965) toward the *petersi* ♀♀.

Eight further sightings of *G. g. serengetae* were made in the study area (Table 2; numbered locations in Fig. 5), all except one concerning single animals. Three records (Nos. 2, 4, 5) could have involved the same ♂ that we saw first, but overall there must have been at least 4–5 different animals. In all cases but one they accompanied a group of Peters' gazelle with which they appeared to be well integrated.

Previously, I had personally seen *serengetae*-type animals only in Tsavo West, ca. 50 km from the first sighting in Tsavo East.

Table 2

Sightings of *G. g. serengetae* in Tsavo East National Park

Numbers refer to localities indicated in Fig. 5

No.	Date	Sex	Age	Remarks
1	20. 4.70	♂	adult	With 1♂ + 2 ♀♀ PG ¹
2	21. 6.70	♂	adult	as above
3	21. 6.70	?	juvenile	alone, ca 500 m from 4 ♂♂ PG
4	16. 2.71	♂	adult	with 1♂ + 3 ♀♀ PG
5	20. 5.71	♂	adult	with 1♂ + 2 ♀♀ PG
6	12. 9.71	?	juvenile	2 animals
7	20.11.72	♂	subadult	with 7 PG
8	3. 6.74	♀	adult	with 10 PG
9	8. 8.74	♀	adult	with 7 PG

¹ PG = Peters' gazelle.

Discussion

Causes of range expansion

Grant's gazelle is a species of fairly to very open habitats and generally avoids well-wooded country (e. g., LAMPREY 1963). In the Tsavo area its occurrence correlates negatively with the density of trees and shrubs (COBB 1976). This supports the assumption, made in the Introduction, that the woodlands which formerly covered much of Tsavo National Park effectively inhibited any large-scale movements out of the presumed original ranges of *G. g. petersi* and *G. g. serengetae*. The drastic reduction in woody cover over the past 25 years (Fig. 3), and the concomitant increase in grass cover, created large tracts of new habitat suitable for Grant's gazelle, particularly in southern Tsavo East. This appears to have led to a considerable expansion of range and, by implication, also of numbers, in *G. g. petersi*, and probably also in *G. g. serengetae*. With respect to the latter, there are virtually no observations documenting the presumed expansion, apart from the sightings of several individuals within Tsavo East.

Routes of movement

The data presented in Table 1 and Figure 5 are consistent with the assumption of a gradual "invasion" of the study area by Peters' gazelle from the east or north-east. We may now ask what routes were followed in these movements. Since detailed observations on the early phases of the range expansion are lacking, this section remains somewhat speculative.

The distribution pattern shown in Figure 4 suggests that the expansion occurred mainly along the larger rivers in Tsavo East (Galana, Voi and Tiva Rivers – Fig. 2). This appears plausible because the vegetation changes began, and have progressed farthest, along these rivers, where elephants tend to concentrate in the dry seasons (see Map 1 of NAPIER BAX and SHELDRIK 1963). Thus, whilst the gazelles are independent of free water and reach their greatest density well away from the rivers mentioned (Fig. 4; COBB 1976), the pattern of their range expansion may have followed the chronology of the vegetation changes, at least approximately. – In addition to elephants, fire played an important part in modifying the original vegetation. Early on, its influence was most pronounced along the eastern boundary of Tsavo East, south of the Galana River (NAPIER BAX and SHELDRIK 1963). Today, some of the most open habitats of Tsavo East are in that area, which also supports the highest density of Peters' gazelle in the new parts of its range (Fig. 4). On the other hand, the blank areas in Figure 4 largely coincide with the densest woodlands remaining in Tsavo East, except for the present study area (X in Fig. 4).

The relatively dense population of Peters' gazelle south of the Voi River may also have provided the recruitment necessary to "invade" new areas, particularly the north bank of the Voi River and the Irima area (Fig. 5).

The question remains as to why the "invasion" of the present study area, before 1973, was not reflected in the aerial counts of 1973/74, on which Figure 4 is based. Probably, this was simply because there were still too few gazelles in the area to be recorded in sample counts with a sampling fraction of only ca. 2.5% (COBB 1976).

The situation in Tsavo West is more difficult to interpret, as no observations of a possible range expansion by *G. g. serengetae* are available. However, one can easily imagine that small numbers of gazelles followed approximately the course of the Tsavo River (Fig. 2) to arrive at the locations in Tsavo East where they were observed.

Long-term outlook

It is tempting to speculate about the eventual consequences of the range expansions described above, particularly about future developments in the zone of contact between the two morphologically distinct and formerly allopatric subspecies of Grant's gazelle. There appears to be a unique possibility of criteria of taxonomic classification being tested against the biological species concept. Because of its distinctive characteristics, Peters' gazelle has been classified as a separate species by a few authors. The brief behavioural interactions observed by us (see above) could mean that the two ♂♂ concerned "treated each other" as conspecifics, although other interpretations are possible. It remains to be seen whether animals of the two subspecies actually interbreed (as they can in captivity – L. DITTRICH, pers. comm.) and have fertile offspring. In this case, the long-term outcome might be some kind of cline from "pure" *petersi* in the north-east to "pure" *serengetae* in the south-west. If, on the other hand, no interbreeding occurs, or with infertile offspring only, classification as two separate species would be justified.

Zusammenfassung

Kontakt zwischen vormals allopatrischen Unterarten der Grantgazelle (Gazella granti Brooke, 1872) infolge von Vegetationsveränderungen im Tsavo-Nationalpark, Kenia

Im Tsavo-Gebiet in Südost-Kenia kommen die beiden Unterarten *Gazella granti serengetae* Heller, 1913 und *G. g. petersi* Günther, 1884 vor. Die letztere scheint bis etwa 1950 nur nördlich des Galana-Flusses aufgetreten zu sein. Die Umwandlung der ursprünglichen *Acacia-Commiphora*-Trockenwälder in offenere Vegetationstypen durch Elefanten und Feuer hat ihr offenbar eine Ausbreitung nach Südwesten ermöglicht. Etwa gleichzeitig sind einige *serengetae*-Tiere aus dem südlichen Teil des Tsavo-West-Nationalparks nach Nordosten vorgestoßen, so daß es zu gelegentlichen Kontakten zwischen den beiden äußerlich gut unterscheidbaren Unterarten kam. In einem Fall wurde eine kurze Kampfszene zwischen zwei ♂♂ verschiedener Unterarten sowie Werbeverhalten eines *serengetae*-♂ gegenüber zwei *petersi*-♀♀ beobachtet.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Erster Lebendnachweis der Etruskerspitzmaus (Insectivora, Soricidae) auf Kreta

VON R. SPRINGHORN UND G. KACHEL

Eingang des Ms. 2.5.1980

Bei VAN DEN BRINK (1972) wird Kreta noch nicht als Bestandteil des Verbreitungsgebietes der Etruskerspitzmaus angegeben. Bereits 1970 konnte indessen SPITZENBERGER aus Gewöllfunden von Kolimvari die Art für Kreta belegen. Umfangreicheres Material aus Schleiereu-



Suncus etruscus bei Paleochora (SW-Kreta). Deutlich abgespreizt der rechte Hinterfuß. (1,6 × nat. Gr.)

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